THORACIC NEUROSECRETORY STRUCTURES IN BRACHYURA.
I. GROSS ANATOMY

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The pericardial plexus in decapod Crustacea was figured and described in several early investigations (Conant and Clark, 1896; Jolyet and Viallanes, 1893; Smith, 1947). Its significance, however, was not recognized until Alexandrowicz (1953) re-examined the structure, demonstrating that it contains not only nerve fibers, but also a number of arborizing terminations located just beneath the sheath surrounding the nerve trunks. This led to the suggestion, substantiated by later experiments (Alexandrowicz and Carlisle, 1953; Maynard and Welsh, 1959), that the pericardial plexus is the terminal portion of a neurosecretory system and is analogous to the sinus gland of the eyestalks. The plexus was renamed the pericardial organ (PO) on the basis of its secretory function.

Alexandrowicz's work left several aspects of the thoracic neurohaemal systems unresolved. This is the first of three papers which re-examine these systems in the brachyurans. It describes the anatomy of three neurohaemal structures in the crab thorax and suggests a correlation between PO volume and aspects of behavior. The second paper of the series will consider the histology and location of neurons contributing endings to the neurohaemal structures. The third paper will describe the histology of the terminations in the pericardial organs.

METHODS

Nine species of crabs from five families were used: Cancridae, *Cancer borealis* (Stimpson); Xanthidae, *Panopeus herbstii* (Milne Edwards); Portunidae, *Callinectes ornatus* (Ordway); Grapsidae, *Grapsus grapsus* (L.), *Plagusia depressa* (Fabricius), *Goniopsis cruentata* (Latreille), *Pachygrapsus crassipes* (Randall), *Gecarcinus lateralis* (Fréminville); Ocypodidae, *Ocypode albicans* (Bosc). The *Cancer borealis* were obtained from Maine (Boothbay Harbor Crab and Lobster Co., Boothbay, Me.), the *Pachygrapsus crassipes* from California (Pacific Biomarine Supply Co., Los Angeles, Calif.), and both were examined during the winter at Ann Arbor. The other seven species were collected and examined at Bermuda during July and August.

Most of the following observations were made upon fresh, unstained material. Where necessary, certain points were confirmed with fresh material stained with methylene blue (Alexandrowicz, 1932) or with preserved specimens. In dissection the dorsal carapace was usually opened, and stomach, hepatopancreas, gonads, and bladder removed to expose the underlying ganglia and ventral thoracic structures. Complete and rapid removal of the hepatopancreas is critical—otherwise powerful digestive juices escape and destroy the finer nerve terminations—but is difficult

because of its delicacy and extensive ramifications. This problem was never completely solved, and prohibits definite statements about the absence of fine nerve branches or the ultimate destination of some nerves. Structures were considered neurosecretory if they appeared bluish-white with incident or darkfield illumination. Where there was doubt during dissection, the structure in question was removed and examined with high magnifications under darkfield illumination. Under these conditions, bluish or greenish colors can be considered a result of scattering or diffraction by small dense granules within the cytoplasm (see Maynard, 1961), and in the present series of investigations were found only in cell bodies, fibers, or terminals which could be termed neurosecretory on the basis of other criteria such as fine anatomy, staining characteristics, or physiological actions (see, also, Brown, 1940; Passano, 1953; Bliss and Welsh, 1952).

Pericardial organs were weighed individually on a fishpole balance constructed from a fine glass rod. One mm. deflection represented about 0.1 mg.; weights were estimated to the nearest 0.02 mg. In every case an attempt was made to include the entire PO but no non-PO material in the final weighing. This was generally believed successful.

Results

Three sites of storage and release of neurosecretory material are located in the crab thorax. Two, the pericardial organs and the anterior ramifications, apparently share some of the same secretory neurons, while the third, the post-commissure organ, is separate. The anatomy of the pericardial organs has been described by Alexandrowicz (1953) and others (Miyawaki, 1955; Matsumoto, 1958), but will be reviewed before proceeding to descriptions of the less known structures.

Pericardial organs

Structure. In the dozen or so brachyuran genera thus far examined, the pericardial organs show a common structural pattern. Typical organs from four species are diagrammed in Figure 1. In every case the PO appears as a plexus of nerve trunks in the lateral pericardium. Following the terminology of Alexandrowicz, this plexus may be divided into an anterior bar region and a posterior bar region, the two being joined by longitudinal trunks. Three nerve trunks pass into the anterior bar region from the ventral nerve mass. The two most anterior enter the lumen of the first branchio-pericardial (b-p) vein some distance from the pericardium; the third enters the lumen of the second b-p vein near its opening to the pericardium. These trunks, with occasional side twigs, run freely in the blood channels to the pericardium where they unite either completely to form a true anterior bar (in *Maia* and *Libinia*) or only partially to form a network of bars (most other genera, Figure 1) which lies across the combined opening of the first and second branchio-pericardial veins. Two nerves pass dorsally from the anterior bar region, one going to the dorsal thoracic muscles and one to the heart as the *dorsal nerve* (Alexandrowicz, 1932). There may be two (*Ocypode, Carcinus, Libinia*) or three longitudinal trunks joining the anterior and posterior bars. These trunks, like the bar regions, may float freely in the pericardial sinus, but often their posterior third is bound to the pericardial wall. The posterior bar lying over the opening of the third branchio-pericardial vein may be simple or complex in form.
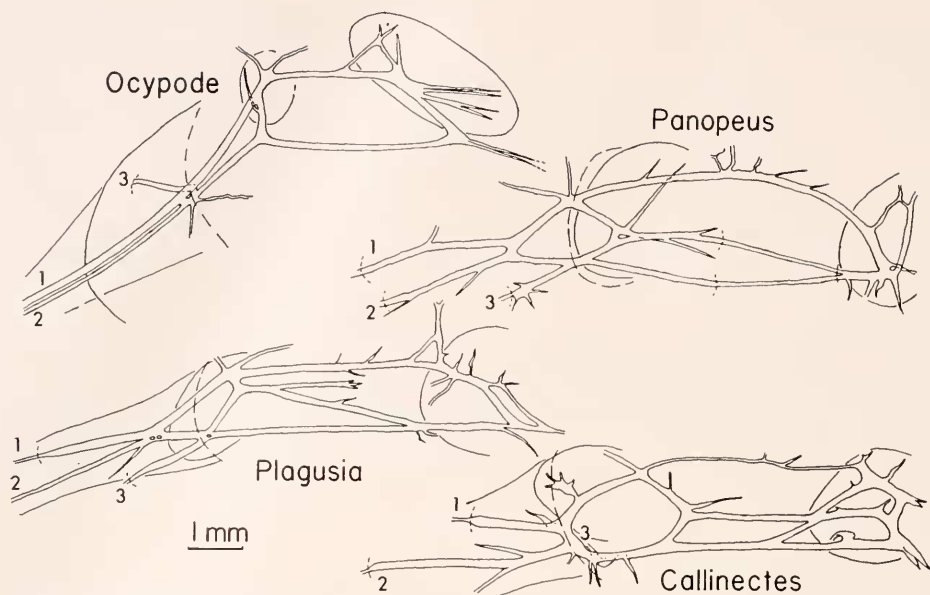
FIGURE 1. Pericardial organs of *Ocypode albicans, Panopeus herbsti, Plagusia depressa,* and *Callinectes ornatus.* Drawings from fresh preparations, organs *in situ* with openings of branchio-pericardial veins indicated. Anterior is to the left. Short dashed lines crossing nerves indicate point of egress from the pericardium or vein, or, in *Panopeus,* regions of two lower trunks which fuse with pericardial wall. The numbers 1, 2, and 3 indicate the first, second, and third segmental nerves, respectively. In the anterior bar region of *Plagusia,* three ovals mark position of anterior neuron cell bodies.

A number of trunks lead from it, some apparently going to the dorsal musculature and some to the ventral thoracic nerve mass as segmental nerves. Little attention has been given these in the present work, but at least some of the branches have been traced and described in *Pugettia* (Heath, 1941). As indicated below, the surface of all free-floating trunks may be considered a potential secretory surface. In addition, some portions of the pericardial lining and ligaments may contain secretory nerve terminations (Alexandrowicz, 1953). These latter areas, however, seem of less importance in the Brachyura than in the Astacura.

Size. Preliminary measurements on *Cancer, Carcinus,* and *Libinia* (Maynard and Welsh, 1959) suggested a correlation between relative pericardial organ weight and habitat or behavior of the species. Weights of pericardial organs were accordingly determined in a series of seven semi-tropical species from varying habitats. The results are given in Table I. The corrected pericardial organ index (weight of one PO divided by body weight, where body weight represents total weight *minus* chelipeds) is significantly higher in active swimming or semi-terrestrial forms such as *Callinectes* and *Ocypode* than in the more sluggish mud crab, *Panopeus.* Intertidal forms such as *Grapsus* and *Plagusia,* or less active terrestrial forms such as *Gecarcinus* fall between (Table II). The PO index showed no systematic variation with sex or with body weight within the samples examined. It may be of interest, however, that the uncorrected PO index (PO weight divided by total

TABLE I

Weight of pericardial organs (PO) in semi-tropical Brachyura

Animal	Habitat	n	Body wt. (gm.)	Total wt. (gm.)	PO wt. (mg.)	PO/BW (10^{-5})	PO/TW (10^{-5})
Ocypode	sandy beaches, above high tide	10	8.1–26.1	14.2–49.4	0.12–0.36	1.58±.23	0.90±.14
Callinectes	shallow bays, brackish	5	36.0–63.4	54.3–104.5	0.50–1.16	1.54±.35	0.99±.23
Gercarcinus	land, burrows	13	16.6–27.1	27.9–48.2	0.12–0.42	1.44±.42	0.87±.24
Goniopsis	mangrove swamps, intertidal	7	8.9–28.7	14.8–55.8	0.12–0.38	1.34±.11	0.76±.11
Plagusia	rocky shores, just below water	10	32.9–50.4	49.8–89.2	0.42–0.72	1.29±.11	0.80±.11
Grapsus	rocky shores, just above water	9	25.6–52.6	42.3–102.7	0.32–0.62	1.23±.17	0.68±.11
Panopeus	shallow bays, muddy bottoms	10	13.8–34.9	26.4–69.9	0.08–0.26	0.70±.21	0.39±.12

TABLE II

Significance levels of comparisons between PO indices of seven Brachyura; determined for corrected (upper) and uncorrected (lower) PO indices by Student's t test

Corrected index: PO/BW

	Ocypode	Callinectes	Gecarcinus	Goniopsis	Plagusia	Grapsus	Panopeus
Ocypode	—	ns	ns	$p = .025$	$p = .005$	$p = .005$	$p < .0005$
Callinectes	ns	—	ns	ns	$p = .05$	$p = .05$	$p < .0005$
Gecarcinus	ns	ns	—	ns	ns	ns	$p < .0005$
Goniopsis	$p = .05$	$p = .05$	ns	—	ns	ns	$p < .0005$
Plagusia	ns	$p = .05$	ns	ns	—	ns	$p < .0005$
Grapsus	$p = .005$	$p = .005$	$p = .025$	ns	$p = .025$	—	$p < .0005$
Panopeus	$p < .0005$	$p < .0005$	$p < .0005$	$p < .0005$	$p < .0005$	$p < .0005$	—

Uncorrected index: PO/TW

TABLE III

Weight of pericardial organs in temperate Brachyura (Maynard and Welsh, 1959)

Species	Habitat	Mean body wt. (gm.)	Mean PO wt. (mg.)	PO/BW (10^{-5})
Carcinus maenas	Maine coast, intertidal	102	0.54	0.53
Cancer borealis	Maine coast, subtidal	351	1.00	0.30
Cancer irroratus	Maine coast, subtidal	214	0.54	0.28
Cancer pagurus	North sea, subtidal	1810	4.0	0.22
Libinia emarginata	Mass. coast, subtidal	647	1.6	0.25
Maia squinado	North sea, subtidal	1560	2.5	0.16

weight, including claws) in the temperate or northern species examined was generally less than that of analogous semi-tropical forms (Table III).

Several factors require that interpretation of the above correlations be made with caution. First, the significant behavioral variable is not certain. Second, histological studies to be reported elsewhere (Maynard and Maynard, unpublished data) indicate that the size of the organ does not necessarily reflect the amount of secretory material contained within it. And third, the pericardial organs do not necessarily represent the only locus for storage and release of neurosecretion in the thorax, and their size alone, therefore, does not reflect the total presumptive storage volume. It seems probable that further information on the physiological function of secretions released from the PO will be necessary before a reasonable evaluation of the significance of the PO index can be made.

Anterior ramifications

Structure. The three antero-ventral trunks of the pericardial organs originate as segmental nerves in the ventral nerve mass. The most anterior of these, the first segmental nerve, corresponds to the cardio-inhibitory nerve, and the second and third to the first and second cardio-acceleratory nerves (Table IV). They leave the ventral ganglia at the level of the second, third, and fourth thoracic segments. The accelerator nerves apparently pass to the pericardium without extensive branching; they contribute fibers to the PO and one fiber each to the dorsal nerve innervating the cardiac ganglion. The inhibitor nerve, however, branches extensively in the region of the muscles supplying the maxillae. This branching forms the *anterior ramifications* (AR), and represents a second peripheral secretory structure (Figs. 2, 3 and 4). A detailed description follows.

Upon emerging from the ventral ganglion mass just behind the integumentary nerve, the first segmental nerve (inhibitor nerve) and integumentary nerve travel

TABLE IV

Terminology of anterior dorsolateral nerves in the decapod thorax

| Genus	Author	Terminology			
Astacus	Keim, 1915	nervus superior primus	nervus superior secundus	nervus superior tertius	nervus superior quartus
Cambarus	Chaudonneret, 1956	nervus superior primus	nervus superior secundus	nervus superior tertius	nervus superior quartus
Cambarus	Wiersma and Novitski, 1942	—	inhibitor nerve	accelerator n.	—
Procambarus	Wiersma and Pilgrim, 1961	—	2nd root, 1st thoracic segment (t.s.)	2nd root, 2nd t.s.	2nd root, 3rd t.s.
Panulirus	Maynard, 1953	—	cardio-inhibitor nerve	first cardio-accelerator n.	second cardio-accelerator n.
Pugettia	Heath, 1941	integumentary nerve	segmental cardiac nerve x	segmental cardiac nerve m	segmental cardiac nerve l
Cancer	Smith, 1947	recurrent cutaneous nerve	inhibitory cardiac nerve	excitatory cardiac nerve	excitatory cardiac nerve
Brachyura	this paper	integumentary nerve	segmental nerve, one	segmental nerve, two	segmental nerve, three
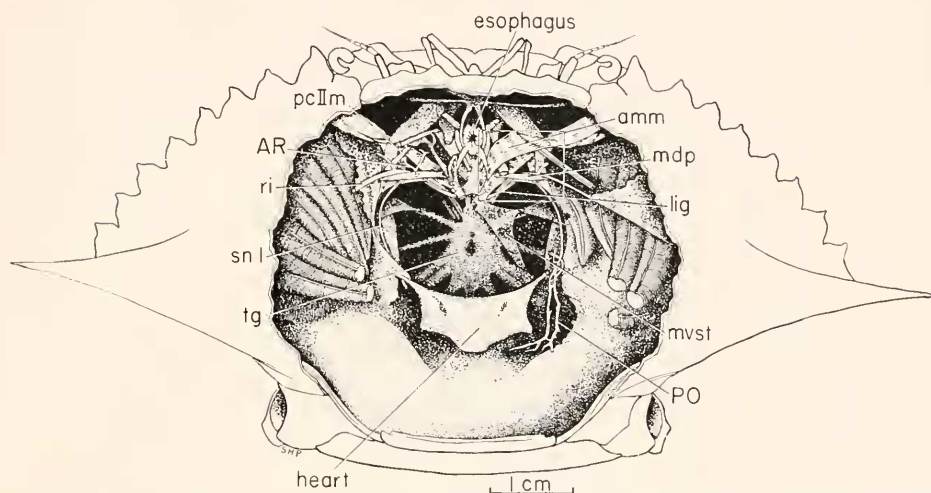
FIGURE 2. Dissection of preserved *Callinectes ornatus* showing location of pericardial organs and anterior ramifications. Digestive gland, stomach, and bladder removed. Amm, musculus abductor maior mandibulae; AR, anterior ramifications; lig, ligament; mdp, musculus dorsoventralis posterior; mvst, musculi ventrales superficiales thoracis; pcIIm, musculus proximalis coxopoditis II maxillae; PO, pericardial organ; ri, recurrent integumentary nerve; sn 1, first segmental nerve; tg, thoracic ganglia. The region bounded by a rectangle to the right of the esophagus is enlarged in Figure 3. Several overlying muscles and ligaments have been removed on the left half of the dissection.

anteriorly and laterally together to the endopleurite of the last head segment. There they pass upward through a ligament loop and angle more laterally toward the musculus dorsoventralis posterior (mdp). The integumentary nerve is often medial and anterior to the segmental nerve at this point. After passing through the ligament loop, and usually before passing beyond the mdp, the first segmental nerve gives off two branches. One angles posteriorly to the muscles attached to ligaments overlying the ventral nerve mass (musculi ventrales superficiales thoracis, Fig. 6), the other larger branch runs anteriorly beneath and beyond the mdp where it proceeds to break up into a network or plexus, the anterior ramifications. These apparently lie beneath a sinus membrane separating the ventral respiratory muscles from the dorsal thoracic cavity. Portions of the AR may dip ventrally in blood spaces between the muscles, or may spread over the membranes covering skeletal elements in the region or over the surface of a nerve (Fig. 3) apparently passing out toward the Y-organ and muscles of the mandible (Echalier, 1959). The form of the AR varies among species; for example, in *Callinectes* the ramifications give the impression of two main branches (Figs. 2 and 3), while in *Plagusia* (Fig. 4) they resemble an irregular net with no obvious main trunk. Most of the branchings and twigs of the ramifications appear to lead nowhere, as in the PO, but there are at least two branches, A and B, in which this is not so. These are particularly obvious in *Callinectes, Plagusia,* and *Eupanopeus.* Branch A separates under the mdp and, travelling medially, appears to enter this muscle near its medial attachment. Its final terminations have not been found. Branch B passes anterolaterally from the ramifications, paralleling the anterior branch of the integumentary nerve.
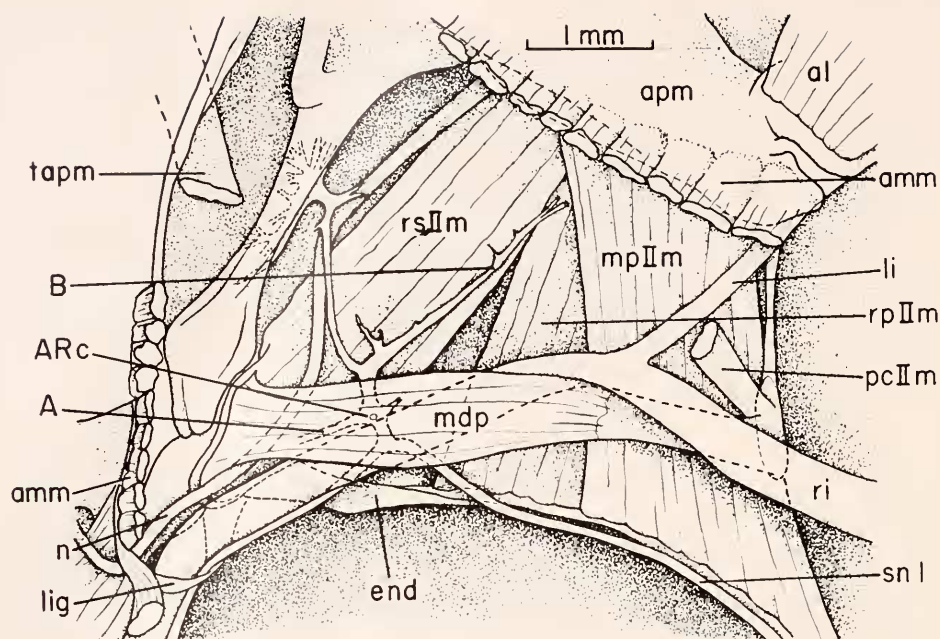
FIGURE 3. Anterior ramifications of *Callinectes ornatus;* fresh material. Dorsal exposure with digestive system removed. A, medial, posterior branch of anterior ramifications; al, musculus adductor lateralis mandibulae; amm, musculus abductor maior mandibulae, only cut segments at origin and insertion remain; the belly has been removed to expose underlying structures. Apm, apophysis of mandible; ARc, location of neuron cell body in anterior ramifications; B, anterior, lateral branch of anterior ramifications; end, endopleurite of last head segment; li, lateral integumentary nerve; lig, ligament; mdp, musculus dorsoventralis posterior; mpIIm, musculus promotor II maxillae; n, anterior dorsolateral nerve of Echalier (1959); pcIIm, musculus proximalis coxopoditis II maxillae; ri, recurrent integumentary nerve; rpIIm, musculus respiratorius primus II maxillae; rsIIm, musculus respiratorius secundus II maxillae; sn 1, first segmental nerve; tapm, stump of tendon of musculus adductor posterior mandibulae. Note how one anterior branch of anterior ramifications spreads over anterior nerve and continues beneath the head apodeme.

In *Ocypode* this branch leads to another more lateral ramification (Fig. 5), but in other species the second ramification seems lacking and branch B disappears among muscles and membranes of the lateral, anterior carapace.

The AR are obviously located in a portion of the venous sinus system. Although the course of haemolymph flow has not been accurately determined in these regions, fluid probably passes over the ramifications as it travels from the general anterior venous sinuses of the thorax to the branchial sinuses in the gills. Perhaps of equal significance is the location of the AR in close proximity to the major respiratory muscles of the scaphognathite. Between them, therefore, the AR and PO are located just upstream from those muscles—respiratory muscles and heart, respectively—which normally exhibit continuous, rhythmic contractions and which are most concerned in the maintenance of adequate oxygen supply to the tissues of the body.

The volume of the AR is less than that of the PO, but its relative size was not measured because of difficulties in removing it without fragmentation.

Post-commissure organs

Although post-commissure organs have been identified in various shrimp and Stomatopoda, there is no published record of their presence in Brachyura. The following account describes them in *Pachygrapsus crassipes* (Fig. 6).

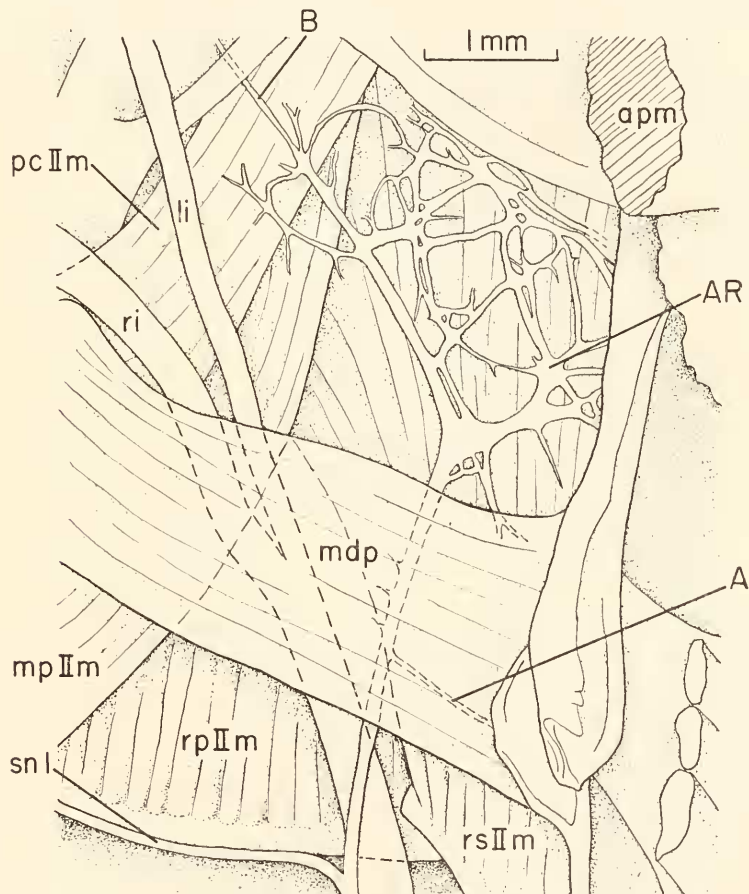In *Pachygrapsus*, as in most other decapods, a pair of post-commissural nerves

FIGURE 4. Anterior ramifications of *Plagusia depressa;* fresh material. Dorsal exposure with digestive system removed; midline to right. A, medial, posterior branch of anterior ramifications; apm, stump of apophysis of mandible; AR, anterior ramifications; B, anterior, lateral branch of anterior ramifications; li, lateral integumentary nerve; mdp, musculus dorsoventralis posterior; mpIIm, musculus promotor II maxillae; pcIIm, musculus proximalis coxopoditis II maxillae; ri, recurrent integumentary nerve; rpIIm, musculus respiratorius primus II maxillae; rsIIm, musculus respiratorius primus II maxillae; rsIIm, musculus respiratorius secundus II maxillae; sn 1, first segmental nerve.
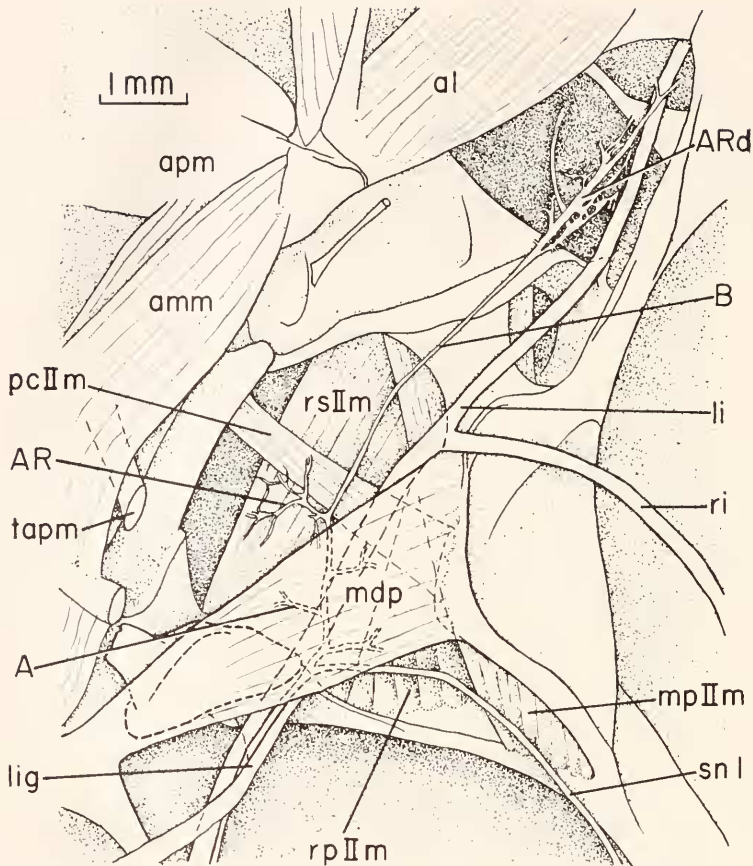
FIGURE 5. Anterior ramifications of *Ocypode albicans;* fresh material. Dorsal exposure with digestive system removed, midline to left. A, medial, posterior branch of anterior rami- fications; al, musculus adductor lateralis mandibulae; amm, musculus abductor maior mandibulae (intact); apm, apophysis of mandible; AR, anterior ramifications; ARd, anterior ramifications, distal segment; B, anterior, lateral branch of anterior ramifications; li, lateral integumentary nerve; lig, ligament; mdp, musculus dorsoventralis posterior; mpIIm, musculus promotor II maxillae; pcIIm, musculus proximalis coxopoditis II maxillae; ri, recurrent integumentary nerve; rpIIm, musculus respiratorius primus II maxillae; rsIIm, musculus respiratorius se- cundus II maxillae; sn 1, first segmental nerve; tapm, stump of tendon of musculus adductor posterior mandibulae.

arises from the post-esophageal commissure. Each of these passes dorsally through the posterior esophageal muscles where it is joined by a major branch of a nerve originating in the homolateral circumesophageal ganglion (see also Fig. 5; Heath, 1941). There are a number of smaller branches from these two nerves which innervate the surrounding esophageal muscles (Fig. 6). In view of the observation that in shrimp the post-commissural nerve does not send fibers to these muscles (Knowles, 1953), it seems possible that a similar situation exists in the Brachyura, and that nerve fibers innervating the esophageal muscles are derived from the nerve

originating in the circumesophageal ganglia and not the post-commissural nerve. The latter nerve passes from the post-esophageal muscles with no apparent diminution in size, and, after travelling laterally for a short distance, divides into two equal branches.   One of these goes forward to terminate in a network of fibers spreading over the anterior third of the ligamentum ventrale capitis.   This network is homologous with the lamellae of the post-commissure organ complex in shrimp and presumably constitutes the storage-release structure analogous to the AR and PO.   It
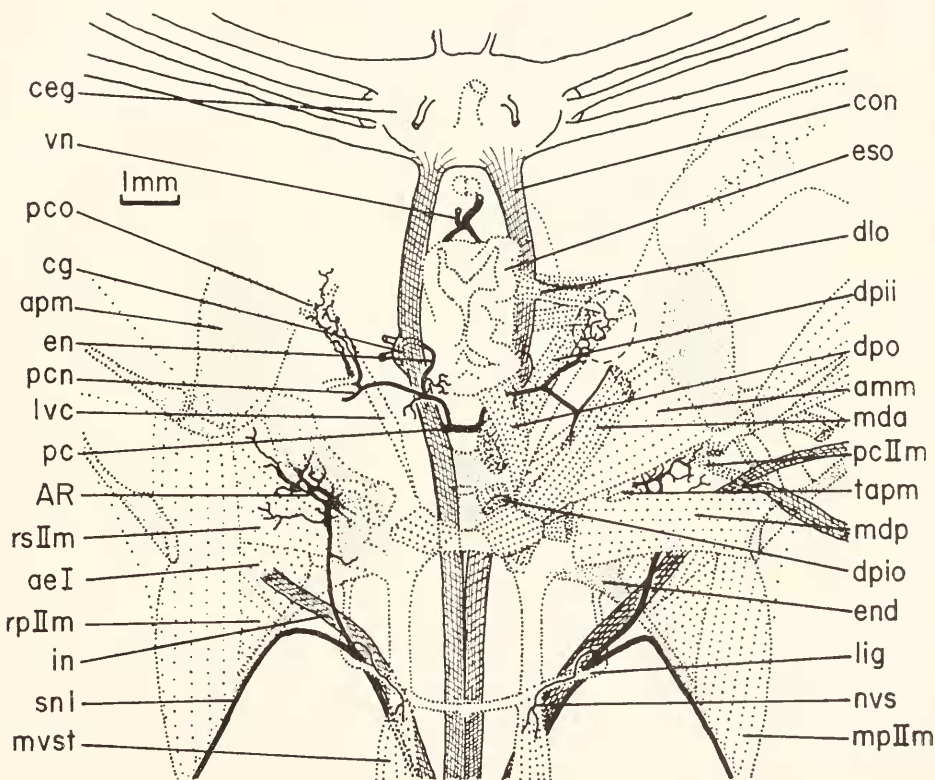

FIGURE 6. Anterior ramifications and post-commissure organs of *Pachygrapsus crassipes;* semi-diagrammatic, from fresh preparation.   Dorsal exposure, digestive system removed.   Ae I, musculus attractor epipoditis I pedis maxillaris; amm, musculus abductor maior mandibulae, apm, apophysis of mandible; AR, anterior ramifications; ceg, cerebral ganglia; cg, connective ganglion; con, circumesophageal connective; dlo, musculus dilatator lateralis oesophagei; dpii, musculus dilatator internus pylorici inferior; dpio, musculus dilatator externus pylorici inferior; dpo, musculus dilatator posterior oesophagei; en, nerve to esophageal muscles; end, endopleurite of last head segment; eso, esophagus; in, integumentary nerve; lig, ligament; lvc, ligamentum ventrale capitis; mda, musculus dorsoventralis anterior; mdp, musculus dorsoventralis posterior; mpIIm, musculus promotor II maxillae; mvst, musculi ventrales superficiales thoracis; nvs, nerve to ventral superficial muscles; pc, post-esophageal commissure; pcIIm, musculus proximalis coxopoditis II maxillae; pcn, post-commissure nerve; pco, post-commissure organ; rpIIm, musculus respiratorius primus II maxillae; rsIIm, musculus respiratorius secundus II maxillae; sn 1, first segmental nerve; tapm, stump of tendon of musculus adductor posterior mandibulae; vn, nerves of visceral system.   The oval bounded by dashed lines above the right post-commissure organ represents the location of a dorsoventral venous channel.
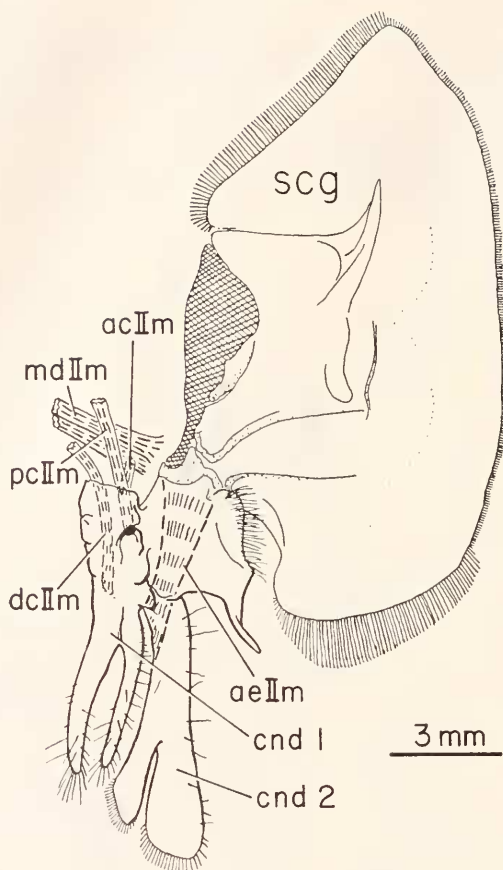
FIGURE 7. Second maxilla of *Callinectes,* showing muscles of coxopodite. AcIIm, musculus adductor coxopoditis II maxillae (no. 60, Cochran) ; aeIIm, musculus adductor endopoditis II maxillae (no. 61, Cochran) ; cnd 1, first endite of coxopodite; cnd 2, second endite of coxopodite; dcIIm, musculus distalis coxopoditis II maxillae; mdIIm, musculus depressor II maxillae (no. 59, Cochran) ; pcIIm, musculus proximalis coxopoditis II maxillae; scg, scaphognathite.

contains secretory granules and will be considered the post-commissure organ. The second branch of the post-commissural nerve innervates a muscle tentatively identified as the musculus dorsoventralis anterior (mda). This is possibly homologous with the "moulting muscle" in shrimp (Knowles, 1953).

In general, the entire anterior-ventral portion of the crab thorax is filled with stomach, hepatopancreas, or ramifications of the bladder. Venous haemolymph flow must therefore be largely confined to channels or spaces among the various viscera. The anterior third of the post-commissure organ is located across such a channel, outlined with dashes in Figure 6, which passes dorsoventrally between bladder protuberances beneath the stomach. Like the other neurohaemal structures of the thorax, the post-commissure organ is in a position to be continually bathed by flowing, venous haemolymph.

In *Pachygrapsus* the post-commissure organ appears the smallest of the three known thoracic neurohaemal structures.

Thoracic musculature

In the course of dissection, several muscles and ligaments were found in the anterior thorax which have not been generally recognized in the Brachyura. Since some of these are in intimate contact with the neurohaemal structures and have been used in the above descriptions or shown in figures, they are listed below with brief mention of their location. Muscles presumed homologous with those described in Macrura are named accordingly (Balss, 1941). Muscles whose homologies are uncertain are named according to their site of insertion.

Musculus dorsoventralis posterior (mdp) (Figs. 2, 6). Origin: ligaments above cephalic apodeme, runs laterally. Insertion: lateral carapace.

Musculus dorsoventralis anterior (mda) (Fig. 6). Origin: ligaments above cephalic apodeme, more medial and posterior than mdp, runs dorso-anteriorly beside stomach. Insertion: dorsal carapace just behind sockets of eyestalks (observed in *Pachygrapsus* and *Cancer*).

Ligamentum (musculus) ventrale capitis (lvc) (Fig. 6). Origin: ligaments above cephalic apodeme, runs anteriorly and slightly laterally. Insertion: carapace at origin of lateral muscles to esophagus. No muscle fibers were found in this structure in the two species examined, *Pachygrapsus* and *Cancer*.

Musculi ventrales superficiales thoracis (mvst) (Figs. 2, 6). Thin, flat muscles overlying thoracic nerve mass in thorax.

Musculus proximalis coxopoditis II maxillae (pcIIm) (Figs. 2, 3, 5, 6, 7). Origin: lateral carapace just anterior to insertion of mdp, runs anteriorly, medially, and ventrally. Insertion: inner membrane of coxopodite of second maxilla (Fig. 7). Apparently pulls coxopodite anteriorly and turns toward mouth (not figured by Cochran, 1935).

Musculus distalis coxopoditis II maxillae (dcIIm) (Fig. 7). Origin: beneath muscle 59, *musculus depressor II maxillae* (Cochran, 1935). Insertion: on medial side of coxopodite of second maxilla, distal to pcIIm. Apparently pulls coxopodite posteriorly and toward mouth (not figured by Cochran, 1935).

Discussion

The observations reported show that the peripheral neurosecretory complex in the brachyuran thorax is much more elaborate than heretofore supposed. Not only are post-commissure organs present as in the Macrura (Knowles, 1953), but the major thoracic neurohaemal structures, the pericardial organs, are but part of a still more extensive system which includes the anterior ramifications.

The total presumptive storage volume for secretion is also relatively large, as may be seen from a comparison between pericardial organs and sinus gland. The PO are the largest neurohaemal structures in the thorax, ranging from 0.25 to 1.0 mg. per 100 gm. total body weight. In *Carcinus maenas* the secretory terminations in the PO trunks form an outer layer which is about 10% of the trunk radius in thickness (Maynard and Maynard, unpublished data). The actual presumptive storage volume of the PO is therefore about one-fifth its total volume, 0.05 to 0.20

mg./100 gm.   This compares favorably with the volume of the sinus gland of the fresh-water crayfish, *Cambarus virilis*, 0.2 to 0.45 mg./100 gm. total body weight (Brown, 1940).

Since functions of the thoracic structures, the PO-AR system in particular, are currently uncertain, some speculation from anatomy seems justified.   Originally, the location of the PO in the pericardium led to the suggestion of a role in cardio-regulation (Alexandrowicz, 1953).   Experiments showing cardio-acceleration by PO extracts supported the suggestion (Alexandrowicz and Carlisle, 1953; Maynard and Welsh, 1959).   It was recognized, however, that the position of the PO is also perfectly suited for release of materials into the haemolymph for immediate distribution over the entire body, and the possibility of more general functions for PO secretion was postulated (Maynard and Welsh, 1959).   The present work strengthens the latter possibility.   Not only is the thoracic system remarkably extensive and voluminous for a cardio-regulatory structure, but branches of the first segmental nerve enter both the PO and AR and single neurons probably have secretory terminations in both structures (Maynard, 1961).   This does not seem efficient if such neurons are concerned only with cardio-regulation, for the AR is located in a passage to the anterior branchial sinus and is separated from the heart by the full length of the afferent and efferent branchial veins.   Such an arrangement is reasonable, however, if PO-AR secretion were indirectly concerned with respiratory transport.   In addition to increased heart rate, one might presume that secretions from the AR portion of the complex play some role in oxygen uptake or circulation in the gills.   Two possibilities may be mentioned.   First, AR secretion may affect ventilation in the gill chamber by acting on scaphognathite muscle activity.   A common hormone affecting both the heart and scaphognathite muscles could provide the loose coordination desirable for optimum gaseous exchange between tissue and external medium.   Second, and perhaps more attractive, AR secretion may alter resistance to haemolymph flow in gill veins (Parrot, 1938).   PO-AR secretions would therefore increase turn-over time by simultaneously increasing heart rate and reducing peripheral resistance.   Increased turnover time would in turn tend to increase oxygen transport rates.

As mentioned earlier, the correlations found between PO volume and apparent activity of the brachyurans examined are interesting, but are very difficult to interpret.   They are in line with the thesis that PO-AR secretions have some function in metabolism, water balance, or stress reactions, but hardly can be accepted as positive evidence.   Appropriate comparative studies on the physiology of the brachyurans involved have not been published.

Summary

1. Three neurohaemal structures occur in the crab thorax: the pericardial organs (PO) in the pericardium; the anterior ramifications (AR) in a ventral sinus near

the respiratory muscles; and the post-commissure organs, lateral to the esophagus and ventral to the stomach. Since the first segmental nerve supplies both PO and AR, the two are considered separate release sites of a single secretory complex.

2. The PO ranges between 0.00025 and 0.001% of total body weight in Bermuda crabs. It is largest in the most active species.

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